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Demographic Studies of Sagebrush Insects as Functions of Various Environmental Factors

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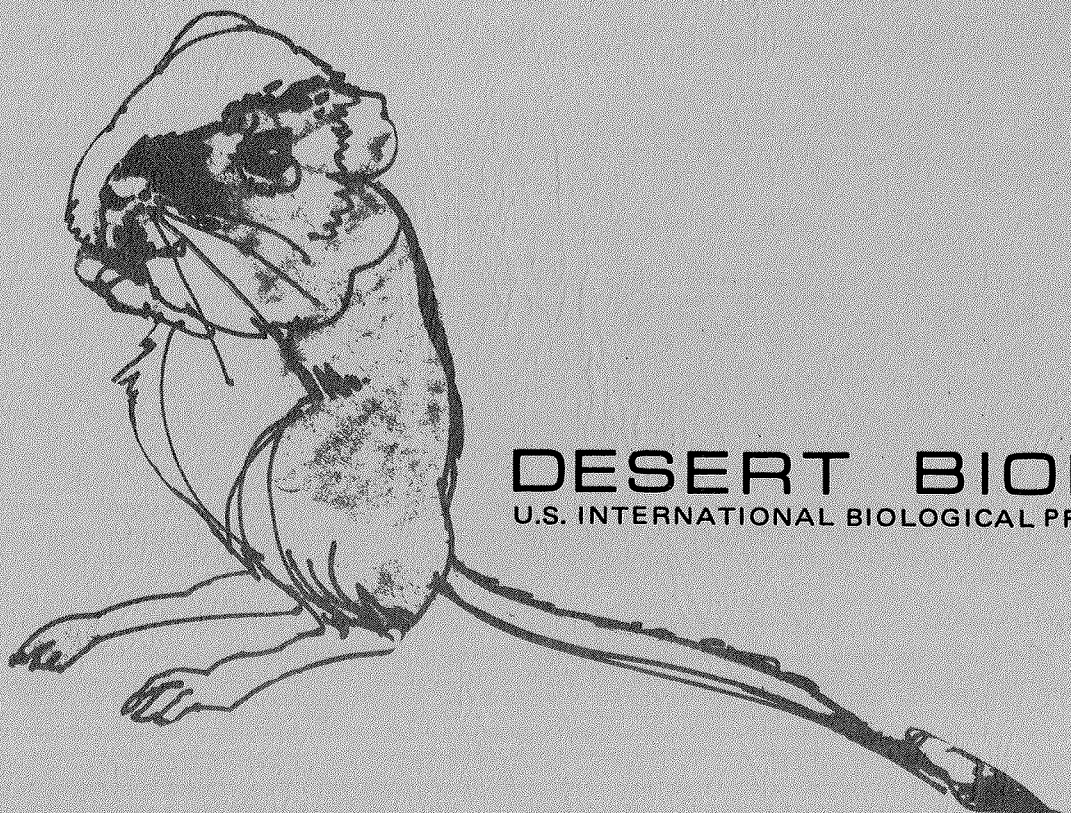

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ABSTRACT

Seasonal history, population dynamics and biology of the sagebrush defoliator, *Aroga websteri* Clarke, were studied at the Curlew Valley site and in the laboratory. The defoliator had one generation a year at the study site. It overwintered in the egg stage. Eggs hatched in the early part of April and larvae passed through five instars between April and June. Pupation occurred from the beginning of June to the middle of July. Adult emergence began in early July and continued until the end of the month. Malaise trap data indicated that adult activity lasted for a period of 2 to 2½ months. Eggs were collected in field samples as early as July 28. Field development of the defoliator was more rapid in 1972 than in 1971. This was due to the warmer weather conditions of April, May, June and July, 1972.

Ten species of parasites were found to attack the defoliator in 1972. Four major species, *Orgilus ferus*, *Phaeogenes* sp., *Spilochalcis leptis*, and *Apanteles cacoeciae*, accounted for over 75% of the total parasitism on the defoliator. Parasitism was rather low in 1972, and increased only from 12 to 24% during the season. As a result, a five-fold increase in the defoliator population was recorded in 1972 over 1971.

Investigations were conducted in the laboratory on reproduction, food consumption and utilization, and effect of temperature on the development of the defoliator. A preliminary version of life tables was constructed from findings of 1971 and 1972 to assess the roles of various mortality factors in the regulation of defoliator population.

A study was conducted to determine the effects of temperature and photoperiod on the development of overwintering first instar larvae of the garden casebearer, *Apterona crenulella*.

INTRODUCTION

Two major sagebrush insects, the sagebrush defoliator, *Aroga websteri*, and the garden casebearer, *Apterona crenulella*, were included in the investigation of 1972. The sagebrush defoliator was the dominant species on the big sagebrush at the northern Curlew Valley site. Therefore, a large share of the research effort was devoted to the study of this species. Field population of the defoliator was unusually high in 1972 as compared to the previous year. This outbreak provided an opportunity to evaluate the impact of several biotic factors, such as predation, competition and adult flight, more effectively than in 1971. Preliminary studies conducted in 1971 provided an understanding of the biology of the defoliator and enabled the development of techniques for rearing and handling this species. Consequently, it was possible in 1972 to conduct several laboratory experiments to obtain biological information that is essential input for demographic studies of the defoliator. Field sampling methods were also improved to allow more efficient collection of samples and a higher degree of accuracy among samples.

The garden casebearer was investigated with a population found in Green Canyon near Logan, Utah. Several experiments have been conducted with overwintering larvae of this species. Data obtained from laboratory studies have provided the basis for prediction of the spring emergence of the larvae and an understanding of the behavior of the species. Results obtained from these studies are discussed in this report.

OBJECTIVES

Most of the objectives outlined in the 1971 report were accomplished in 1972. The lack of sufficient manpower necessitated a delay in the field study of the garden casebearer.

The following objectives have been pursued in 1972:

1. To determine seasonal history and natural mortality of the sagebrush defoliator.
2. To conduct laboratory studies to determine the effects of environmental factors on development of the two sagebrush insects.
3. To determine the food consumption and utilization by the defoliator.
4. To estimate the quantitative relationships between population size of defoliators and the degree of sagebrush defoliation.

Aroga websteri

METHODS

Sampling procedures

Samples of the immature stages of the defoliator were collected weekly to determine the seasonal history and population density of this insect. The data were also used for analysis of the dynamics of the defoliator population.

Statistical analysis of the sampling procedure conducted in 1971 revealed that a smaller sample unit could be used and a higher level of reproducibility obtained for the same cost effort. Therefore, two alterations were made in the sampling procedure in 1972. The study plot of 100 m^2 was divided into quadrant blocks, and ten plants were selected randomly within each designated block. A representative branch that extended from the ground level to the height of the plant was selected. The branch was then cut off at ground level, weighed, labeled, and placed in a plastic bag. In the laboratory the samples were examined by shaking the foliage and picking through it with forceps. The numbers and stages of the defoliator were determined. The population density was then expressed in terms of the number of defoliators per kg of fresh sagebrush.

Rearing techniques

Defoliators obtained from field samples were reared in the laboratory. First and second instar larvae were transferred to small plastic cages 2 cm high and 3 cm in diameter with moist filter paper at the bottom. Moisture apparently was important for the establishment of the young larvae, as those placed in containers lacking moist filter paper soon became desiccated. Ten of these cages were mounted on a 7 x 19 cm plexiglas sheet and the tops of the cages covered with tight-fitting plastic lids. Ten larvae were placed in each cage along with 3 or 4 small, tender leaves from the tips of sagebrush plants. The leaves were changed approximately every 3 days to prevent growth of mold.

Third instar larvae were transferred to larger plastic containers, 6 cm high and 5 cm in diameter, for the remainder of larval development. These cages were fitted with nylon cloth tops which were secured with elastic bands. Ten to twenty larvae were placed in each container and supplied with fresh leaves as needed. All cages were placed in a Percival environmental growth chamber maintained at 30 C, a relative humidity of approximately 50 to 60%, and a photophase of 16 hr.

Pupae were separated from the larvae and held in a large container inside the growth chamber. Upon emergence the moths were transferred to oviposition cages for further study.

Effects of temperature on development of immature stages were investigated with a group of 300 first instar larvae collected from the study site on 22 April, 1972. These were transferred to the small plastic cages previously described. Originally ten larvae were placed in each cage. As they became larger, they were divided into smaller groups to minimize the effects of crowding. The larvae were separated into three groups of one hundred larvae each, and each group was reared in a different growth chamber. The temperatures of the growth chambers were set at 21, 26.5 and 30 C; the relative humidity ranged from 50 to 60%. All growth chambers were set at a photophase of 16 hr.

Larval mortality ususally increased if the insects were removed from their feeding sites frequently, so only ten insects in each growth chamber were examined each day. Records were kept of the daily development of the sampled larvae at each of the given temperatures.

Measurement of adult activity

Two methods were used in studying adult activity in the field. A Malaise trap was erected in late June near the study plot and weekly records were kept of the number and sex ratio of moths collected. The height of moth flight was determined by placing sticky traps at the study site from 14 to 28 July, 1972. Three boards 2 m in length and 20 cm in width were painted with Stickem^{R}. These boards were secured in an erect position by metal stakes and placed in the study site. Weekly counts were made of the number of moths captured on the board at 5 cm intervals.

Oviposition studies

In 1971, attempts were made to sample defoliator eggs in the field. This approach proved unsuccessful because eggs are deposited under sagebrush bark and are quite obscure. The sampling was also very tedious and quite inadequate. In 1972, two methods were used to calculate the fecundity of the females. The first method involved a direct count of the total number of eggs laid by individually-caged females.

An indirect method was also used to determine fecundity. Weekly records were kept of the ovarian development of females captured in the Malaise trap used for adult activity studies. Generally, ten females were dissected weekly and the number of differentiated oöcytes was recorded, thereby allowing an estimation of the number of eggs laid per female.

Food consumption and utilization

Food consumption and utilization of fourth and fifth instar larvae were determined by the use of a gravimetric method (Waldbauer, 1966). Twenty five newly-molted fourth instar larvae were individually weighed and placed in small plastic cages. The cages were then transferred to a growth chamber where a temperature of 30 C and a relative humidity of about 50 to 60% were maintained. The larvae were fed with 3 or 4 pre-weighed leaves obtained from the same leaf cluster. Leaves were changed at two-day intervals. Since the dry weight of the leaves could not be determined before feeding, an estimation of the percent dry matter of leaves was determined from an aliquot. Each time fresh leaves were provided, the weights of uneaten food, fecal matter, and larval weight gain were recorded. On the basis of the results obtained, approximate digestibility (A.D.), efficiency of conversion of ingested food (E.C.I.), efficiency of conversion of digested food (E.C.D.) and consumption index (C.I.), were calculated for the two larval instars.

Defoliation studies

Defoliation studies were conducted in early July, 1972. At this time the damage caused by the sagebrush defoliator had reached a maximum for the season. Twenty-six plants were selected within the study area that represented a range from slight to complete defoliation. These plants were cut off at ground level, weighed, labeled and placed in plastic bags. In the laboratory, the number of defoliators found on each plant was recorded. The damaged leaves were separated from the undamaged leaves and both were dried to constant weight. The ratio of damaged to undamaged leaves was used to calculate the percent defoliation.

The effects of defoliator density on the sagebrush plant were also studied in the field using caged plants. Four defoliator-free plants were selected near the study site and individually enclosed in nylon cages, 1 x 1.5 x 2 m. Third and fourth instar larvae collected from the study site were divided into groups of 100, 200, 300 and 400, and placed on the caged plants of 5 May, 1972. On 1 July, the plants were removed from the cages. The numbers of pupae and pupal cases were counted and the percentage of defoliation was determined by the method described previously.

RESULTS AND DISCUSSION

Seasonal history

The sagebrush defoliator had one generation at the study site in 1972. Table 1 summarizes the data from field sampling of different age groups of the defoliator and

the population density throughout the season. These data are graphically represented in Figure 1, to illustrate in relative percentages the progression of development of these age groups. Data collected in 1971 are presented in Figure 2 to provide direct comparison.

Table 1. Age structure and population density of *A. websteri* at Curlew Valley site, 1972 (DSCODE A3UHL01)

Date of sampling	Egg	Larval instar					Pupa	Pupal case	Total	Total defoliators per kg fresh sagebrush
		1st	2nd	3rd	4th	5th				
April 22		758	487	76	7				1328	108.8
May 6		255	504	171	7				937	115.3
May 11		156	516	143	4				819	135.9
May 20		6	172	726	428	13			1345	164.6
May 25			62	455	430	32			979	173.0
June 2				116	653	408			1177	170.7
June 9					238	716	1		955	152.0
June 15					59	689	24		772	150.1
June 22					2	543	98		643	148.3
July 1					4	308	276	9	597	129.8
July 7						50	463	37	550	113.2
July 14						1	293	128	422	100.5
July 16							16	99	115	97.4
July 28	87						4	116	207	-
Sept. 6	92								92	-
Oct. 5	21								21	-

Field sampling conducted in the spring and fall of 1972 revealed that the defoliator overwinters in the egg stage at the study site. The embryos are fully developed, but apparently remain within the chorion until early spring. The study site was inaccessible for sampling until late April due to early spring rains. The first field samples were collected on 22 April. At this time, over 50% of the defoliators were first instar larvae. The increase in the larval population during the subsequent samplings indicated that egg hatching might have continued until the latter part of May. Larval development in the field was earlier and faster in 1972 (Figure 1) than in 1971 (Figure 2). These differences in development rate were due

to the higher mean temperature during the months of May, June and July, in 1972. An analysis of the long-term mean temperature for these three months revealed that a -0.8 C below mean was recorded in 1972 as compared to a -1.1 C below mean in 1971. These measurements were taken at Snowville, Utah, the closest weather station to the site.

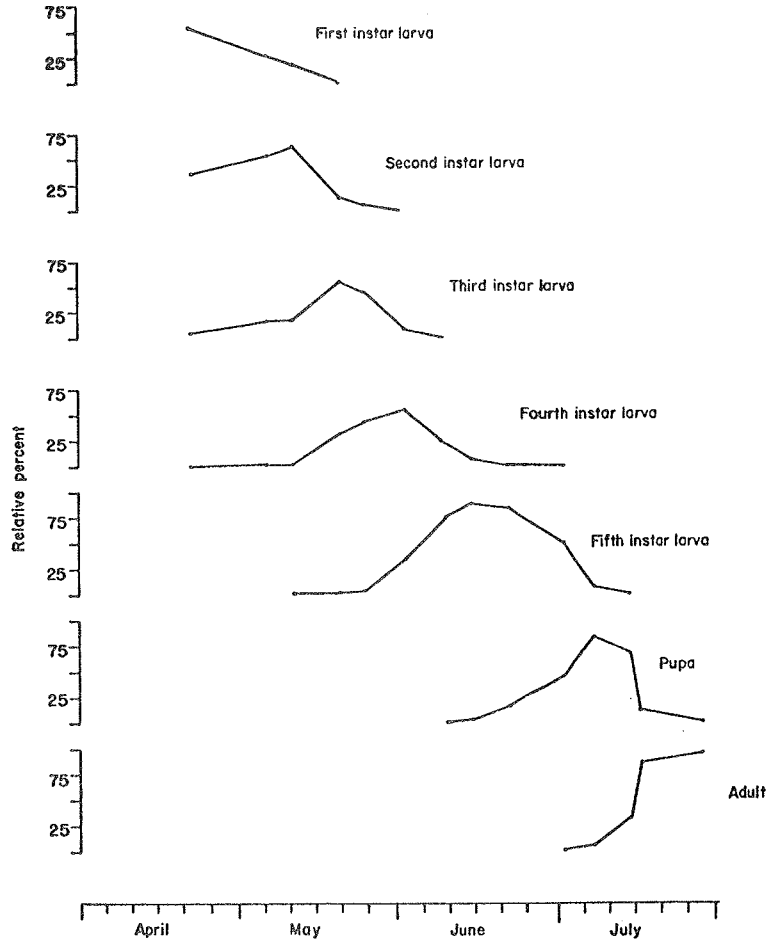

Figure 1. Age structure of *A. websteri* population at Curlew Valley site, 1972. Data obtained from successive sampling dates were calculated as relative percentages of each age class.(DSCODE A3UHL01)

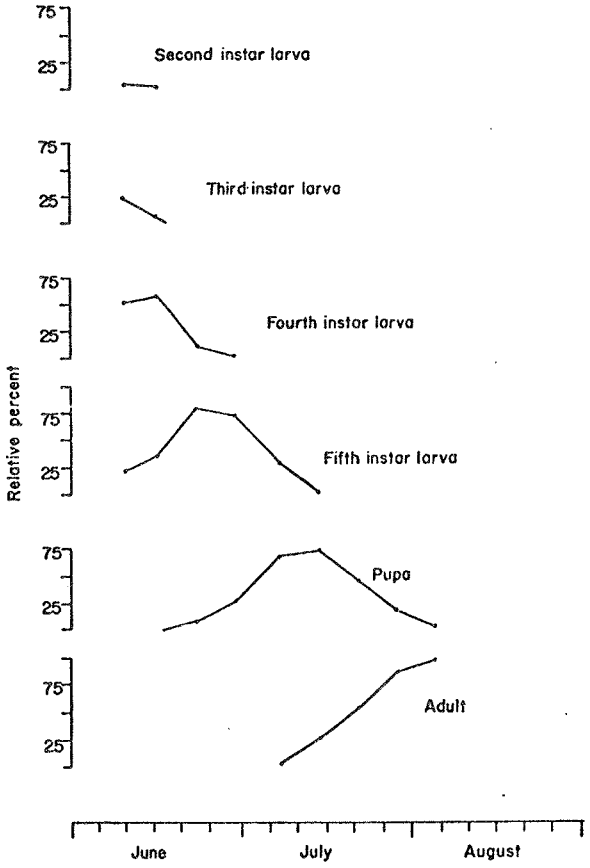

Figure 2. Age structure of *A. websteri* population at Curlew Valley site, 1971. Data obtained from successive sampling dates were calculated as relative percentages of each age class (DSCODE A3UHL01)

The population density of the defoliator, based on the number of individuals per kg of sagebrush, was also found to be about 5 times greater in 1972 than the previous year. As a result of high defoliator population, a general occurrence of sagebrush defoliation was noticeable at the study site.

Biology

Egg: Eggs are generally laid under the light gray bark immediately below the sagebrush foliage, and are occasionally found on outer bark surfaces. Stems of less than one-fourth inch in diameter are preferred for egg laying. Eggs are attached to the plant tissue by a viscous and transparent substance, and are difficult to remove. Although the eggs are laid singly, often small groups of 2 or 3 eggs were found under field conditons. Newly-deposited eggs are clear white in color and later change to a creamy yellow. Embryonic development apparently begins immediately when the eggs are laid. The U-shaped embryo was observed within the egg shell after a two-week incubation at 30 C. Chilling of 100 of these embryonated eggs at 2 C for a 3-week period and then subjecting them to several weeks of incubation at 30 C and a photoperiod of 12 hr of light did not initiate hatching. It can be assumed that the eggs had entered a true diapause. The egg diapause could be broken by rupturing the chorion. Once disturbed, the larva crawled out of the chorion and soon searched actively for feeding sites. The larvae obtained in this manner were unable to establish themselves on sagebrush clippings and eventually died.

Larva: Newly-hatched larvae collected from the field are pale yellow with a dark brown head capsule and cervical shield. The thoracic legs are strong, enabling the larvae to cling to surfaces readily. When placed on caged plants the young larvae were observed to move briskly about the sagebrush leaves until a feeding site was secured. Fifty young larvae placed on a grid travelled an average distance of 5 cm in 5 minutes. It was also noted that they were attracted toward light, and moved upward when placed on an inclined surface. These three factors probably contribute to rapid larval establishment on foliage tips. Under laboratory conditions, however, the newly-emerged larvae had some difficulty in establishing a feeding site. Generally, 1 to 1½ days were required for healthy larvae to begin feeding on sagebrush clippings.

The larvae first attacked the young leaves near the terminal tips of the plants. Initially they produced webbing encompassing 2 or 3 leaves, but the feeding site gradually enlarged during the season.

Whether the larvae completed development and pupated near the original feeding site, or migrated to other branches, largely depended upon the amount of foliage available. Larvae placed on caged plants were observed to migrate to surrounding branches as defoliation increased. In the field, mature larvae were also observed to move to neighboring plants during extensive defoliation.

Larvae generally formed web tubes which extended from the main webbing site to the terminal ends of several branches. This enabled them to feed on the surrounding leaves and remain within the protective webbing. When disturbed, the larvae moved rapidly back into the tube or dropped to lower branches by a single silk thread.

As the larvae developed, the webbing extended in length to encompass new plant growth. The web tubes of the mature larvae were 5 to 8 cm in length, but occasionally extended to 10 cm. As the season advanced, larvae tended to congregate among the remaining foliage. Prior to pupation the larvae formed a loosely-webbed cocoon and were quiescent. First instar larvae collected from the study site were reared at constant temperatures of 30, 26.5 and 21 C. The time required to reach the adult stage was 27-34, 30-35 and 40-50 days, respectively.

Pupa: The pupae were initially a light brown in color, but gradually became darker prior to adult emergence. The pupal sizes and weights varied considerably with the food intake of the larvae. Measurements of 25 pupae collected in the field produced the following means: length, 6.6 ± 0.9 mm; width, 2.1 ± 0.3 mm; fresh weight, 7.8 ± 1.2 mg.

Adult: The adult wing span ranges from 13 to 16 mm. The front pair of wings is stippled with black markings and fringed about the outer margins. The hind wings are a lighter gray color and more heavily fringed than the front pair. The male and female are similar in appearance, although the female abdomen is generally larger than that of the male. Claspers also characterize the distal end of the male abdomen.

A total of 2761 moths was captured during the 1972 season. These data are summarized in Figures 3 and 4. Adults were first found in the Malaise trap at the beginning of July, which was about the time that pupal cases were recorded in field samples (Table 1). The number of moths captured gradually increased until it reached a peak in the last week of July, which also coincided with the largest number of pupal cases collected in the field samples. Since this peak number of adults found in the Malaise trap continued at about the same level for approximately 3 weeks, it can be assumed that the adults live for at least this period.

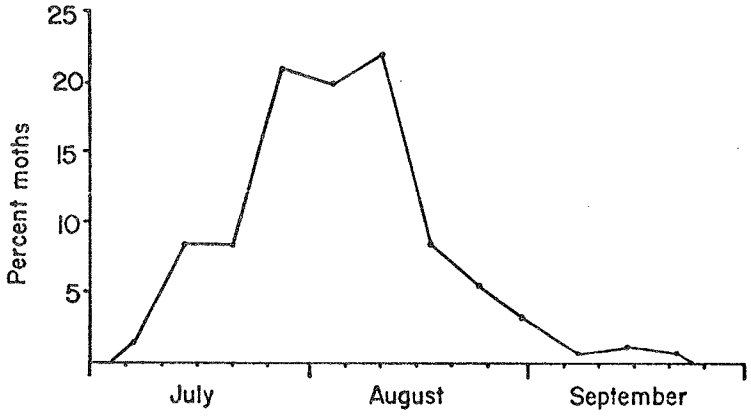

Figure 3. Weekly record of *A. websteri* moths captured in Malaise trap at Curlew Valley site, 1972.

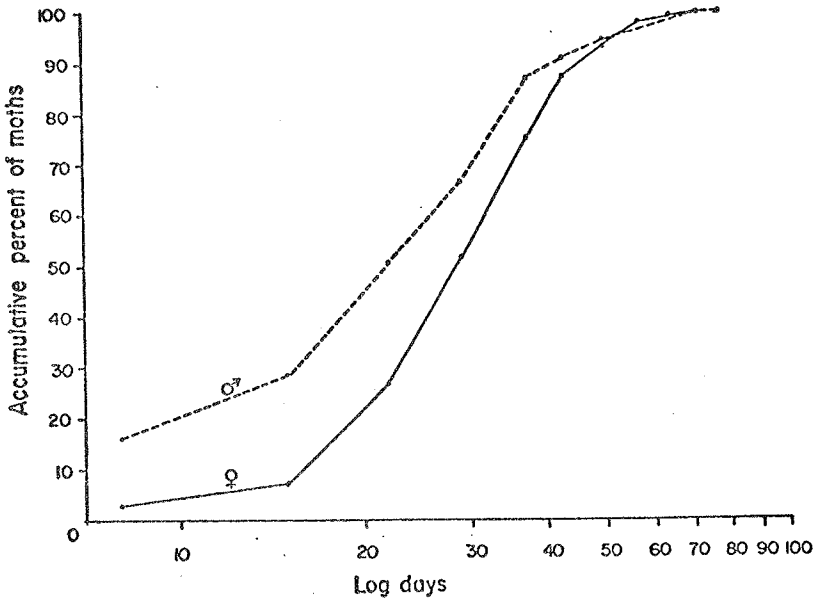

Figure 4. Weekly record of male and female *A. websteri* moths captured in Malaise trap at the Curlew Valley site, 1972.

Data from laboratory rearing of 345 pupae and the Malaise trap data (Figure 4) show a tendency toward a higher ratio of males to females (5 to 1) at the early part of adult emergence. This difference gradually diminished until a sex ratio of 1:1 was reached. On the basis of these data, it can be inferred that the Malaise trap data provide an accurate estimation of adult activity in the field.

Adult moths have functional mouthparts and a complete digestive tract. A 10% solution of equal amounts of honey and sucrose was made available to caged moths, and they were frequently observed to feed on this solution. It is not known whether feeding enhances copulation, oviposition or embryonic development in the eggs, but adults provided with the honey-sucrose solution lived for an average of 2 to 3 weeks longer than unfed moths. Caged females lived for as long as one month. In the field, a plant that possibly may have provided nectar as food for the moths was rabbitbrush. This plant was observed to flower during the time of moth flight, and sticky traps placed among rabbitbrush blooms captured as many adults as those placed among sagebrush branches.

The moths spend the day quietly hidden under bark or in debris beneath the plants. Adults placed on caged plants became active 2 to 3 hr following dusk, and reached maximum activity between 2300 and 0500 hours. The moths were observed to move erratically over the bark and leaves of the plants. When released from the cage they flew rapidly in a zig-zag course and landed nearby. Flight activity decreased at sunrise, and the moths gradually dispersed to various hiding places and remained there for the duration of the diurnal period.

Figure 5 compares the height of sagebrush plants at the study site and the number of defoliator adults captured on sticky traps at various heights. The results show that the height of moth flight closely follows the height of the sagebrush. The majority of the moths were captured between 30 and 80 cm above the ground surface, and only a few individuals were found at a height of 120 cm. It can be concluded that moth activity in the field was generally concentrated about the periphery of the sagebrush crown.

Reproduction: Female moths have two ovaries, each with four ovarioles. Upon adult emergence, none of the 7-12 visible oöcytes is fully-grown. The largest oöcyte is approximately 0.120 mm in width, and the ovarioles become gradually narrower towards the anterior. An additional number of undifferentiated cells is present in the suspensorial apparatus of the ovary. During the oviposition period the last egg of each tube is abruptly larger than any of those preceding it (usually 0.360 mm wide by 0.601 mm long).

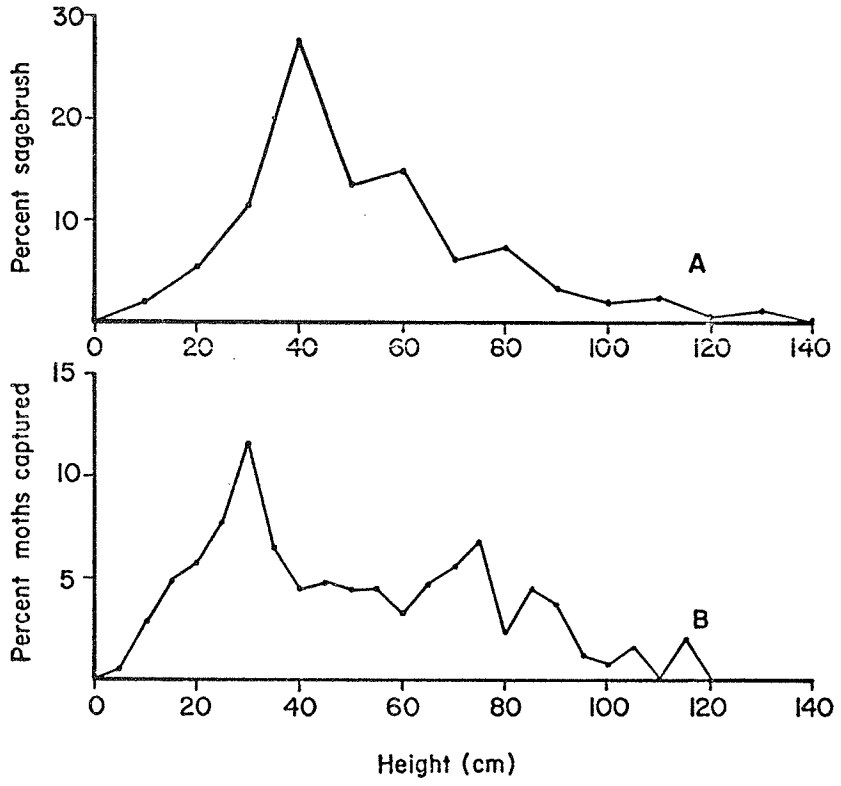

Figure 5. Comparison of the height of sagebrush to *A. websteri* moths captured at various heights. A. Percentage of sagebrush at given heights. B. Moths captured as determined by sticky trap collections. Curlew Valley site, 1972. (DSCODE A3UHL03)

All females captured in the Malaise trap were gravid. Therefore, egg production is assumed to be continuous during the active part of adult life. Examination of 50 females produced 2-16 fully-grown oöcytes per ovary, with a mean of 9.8. The maximum number of differentiated oöcytes found within a single ovariole was 15; therefore the potential production would be 120 eggs. However, this is only an estimation because oöcyte production in the female was continuous.

A direct count of the number of eggs laid by caged females was also taken to estimate fecundity. Eighteen females were individually confined in 1.9 liter cylindrical cages containing sagebrush plants. Only 8 of the females thus caged deposited eggs. Two females that were kept in larger cages (30 and 45 cm^3) deposited 81 and 84 eggs, respectively. These preliminary data indicate that cage size is an important factor in reproductive success of the female.

A variety of surfaces such as filter paper, debarked stems, paper towels, and tree bark were provided to caged moths for egg laying, but none was observed on these substrates. Apparently, physical texture or chemical stimulation are required to initiate egg laying. Moths were found to lay eggs readily on dead sagebrush branches in the laboratory and under field conditions. However, the proportion of eggs deposited on dead vs. growing plants is not known.

Natural enemies

Ten parasites were found to attack the sagebrush defoliator at the study site. These were *Apanteles cacoeciae* Riley, *Orgilus ferus* Mues., *Meteorus* sp., and *Microtypus* sp. (Braconidae); *Phaeogenes* sp., *Diadegma* sp., and *Temelucha* sp. (Ichneumonidae); *Copidosoma bakeri* (Howard) (Encyrtidae); *Microdontomerus* sp. (Torymidae); and *Spilochalcis leptis* Burks (Chalcididae).

Detailed data on the percentage of parasitism due to these parasites are summarized in Table 2. As a whole, percent parasitism was lower in 1972 than in 1971. *O. ferus* was the most common parasite in 1971 and caused mortality of approximately one-third of all fifth instar larvae. However, in 1972 the incidence of parasitism by this species was much lower. Muesebeck and Walkley (1951) reported that parasites of the genus *Orgilus* have been reared from species of five lepidopteran families. Therefore it is likely that the defoliator is not the only host for this parasite.

Phaeogenes sp. and *S. leptis* both oviposited in young host pupae. These parasites fed internally until they emerged as adults in early to mid-July. Both species are considered to be important parasites of the defoliator.

Apanteles sp. attacks either the egg or the young larvae of the defoliator. The parasites emerged from fourth instar larvae in mid-June and spun a white silken cocoon within the defoliator feeding site. Prior to this time they were not visible within the host.

Copidosoma bakeri was believed to attack the egg stage, although some early rearings in 1972 did not contain this parasite. King and Atkinson (1928) reported that this species oviposited in the eggs of *Euxoa ochrogaster*, but that the parasite did not begin development until the host larvae were in the last instar. This is also assumed to be the case with the defoliator.

Table 2. Parasites of *A. websteri* reared from field samples

	No. hosts reared	No. non-parasitized hosts	No. parasitized hosts	*Apanteles cacoeciae*	*Temelucha* sp.	*Orgilus ferus*	*Copidosoma bakeri*	*Phaeogenes* sp.	*Spilochalcis leptis*	Other*	Total % Parasitism
1971											
June 10	73	40	10	4.0	10.0	4.0	2.0	0	0	0	20.0
16	98	52	23	1.3	9.3	17.3	1.3	0	0	1.3	30.5
23	205	120	111	1.3	10.0	32.9	2.2	0.9	0	0.9	48.2
30	201	87	123	0	0	29.5	1.9	15.7	8.7	2.8	58.6
July 7	327	68	211	0	0	55.6	0.7	11.8	7.2	0.4	75.7
14	296	138	153	0	0	0	0	34.7	16.8	1.0	52.5
21	45	26	10	0	0	0	0	16.7	11.1	0	27.8
1972											
Apr. 22	605	145	21	9.6	3.0	0	0	0	0	0	12.6
May 6	510	130	52	17.6	0	5.5	5.5	0	0	0	28.6
11	553	158	25	9.8	2.2	0.5	1.1	0	0	0	13.6
20	971	377	119	18.3	2.0	2.2	1.0	0	0	0.4	23.9
25	950	372	118	15.1	2.4	1.6	2.4	0	0	2.4	23.9
June 2	1107	565	103	8.5	2.2	1.3	1.8	0	0	1.5	15.3
9	873	667	45	2.0	0.6	1.0	2.0	0	0	0.8	6.4
15	707	493	46	0.9	0.4	1.7	3.3	0.7	0.6	0.9	8.5
22	521	304	49	0	0	0	5.4	2.0	4.2	2.2	13.8
July 1	580	309	77	0	0	0	4.4	6.5	9.1	0	20.0
7	570	401	82	0	0	0	5.1	11.1	0.6	0.1	16.9
14	200	160	21	0	0	0	0	4.4	7.2	0	11.6
16	16	3	1	0	0	0	0	0	2.5	0	2.5

* *Diadegma* sp., *Microdontomerus* sp., *Meteorus* sp., *Microtypus* sp.

Two species of hyperparasites were encountered during both 1971 and 1972; they were *Catolaccus aeneoviridis* and *Gelis* sp. *C. aeneoviridis* was found to attack *O. ferus*, *Diadegma* sp., *Temelucha* sp.,*S. leptis*, and *Phaeogenes* sp. Between 20 and 28% of these primary parasites were destroyed by this species. The incidence of hyperparasitism by *Gelis* was not high enough to be recorded.

Fillmore (1965) recorded 18 species of Hymenoptera and one species of Diptera as parasites of the defoliator in southern Idaho. Of these parasites, seven species were recorded in the rearing of defoliators collected from northern Curlew Valley. The other three hymenopterous species, *Microdontomerus* sp., *Meteorus* sp. and *Microtypus* sp., are new records of parasites of the defoliator.

Larvae of a chrysomelid beetle, *Phyllobaenus* sp., were occasionally found feeding on the larvae or pupae of the defoliator. The adult stage was never found to attack the defoliator. The actual impact of this predator on the population dynamics of the moth is assumed to be minimal. Field samples showed an average of 1 beetle larva per 26 defoliators in 1971 and 1 per 125 in 1972.

A microsporidian was found to attack the larval and pupal stages in the field and in the laboratory. Infected larvae became sluggish and stopped feeding after they were infected. The integument became soft-textured and the larvae turned a characteristic dark color. The integument did not rupture following death, but hardened and became distinctly brittle. When diseased larvae were dissected and examined under the microscope, the gonads and fat bodies were found to be teeming with the protozoan. Often the fifth instar larvae were able to pupate, but the adults failed to emerge.

The egg tubes of infected females became sac-like chambers which were filled with protozoa. Usually only one or two oöcytes remained intact. The crowded condition of the host during 1972 probably promoted wide dissemination of spores, although the microsporidian was able to manifest itself also during the low population level of 1971. Under laboratory conditions, a high mortality rate of 4th and 5th instar larvae was due to parasitism by the microsporidian. However, mortality due to this cause rarely exceeded 5% in the field.

Life tables

On the basis of field and laboratory data collected in 1971 and 1972, preliminary life tables were constructed to define the various mortality factors within specific age intervals (Harcourt, 1969).

The sampling period of the defoliator was divided into five intervals. This was based on the similarity of the "crucial trials" through which the insects must pass if they are to survive. The five intervals are: larvae, period 1; larvae,

period 2; larvae, period 3; pupae; and adult (at emergence). Table 3 and 4 show the values for two generations of the defoliator. The column headings are those proposed by Morris (1963).

Larvae, period 1 (Instar 1, 2 and 3): The l_x was obtained by population sampling in early June, 1971, and mid-April, 1972. The actual number of larvae entering this period was not determined, but the l_x was calculated by graphic summation as outlined by Southwood and Jepson (1962). The principal mortality factor during this interval was assumed to be the failure of larvae to become established on the sagebrush foliage. The exact environmental factors responsible for the mortality were not determined. Mortality was not caused by parasite emergence during this period. The young larvae rarely encountered diseases and predation was minimal.

Larvae, period 2 (Instar 4): The larvae were well established on the sagebrush plants. Collections were made at the beginning, middle, and end of the fourth instar and the larvae were reared to establish the incidence of parasitism. The effect of the factors of competition and overpopulation varied with the amount of foliage available to the defoliator.

Larvae, period 3 (Instar 5): The l_x was determined by a series of population samples prior to and during the fifth instar development. Parasites, pathogens and food shortage accounted for a significant population reduction during this period. Starvation became significant with the increase in defoliators during this age interval.

Bird predation was not an important mortality factor as indicated by lack of defoliator head capsules in 150 bird droppings collected in the study site.

Pupae: The l_x for the pupal stage was determined by direct field counts prior to and during moth emergence. Pupae were transferred to the laboratory where the incidence of parasitism was determined. Predation by beetle larvae was detected by examination of the pupae for beetle feeding marks.

Adults (at emergence): The adult l_x was determined by examination of pupal cases in the field for evidence of normal ecdysis. Infertility caused by microsporidia was determined by dissection of 50 moths which were captured at the study site. The mortality factors listed for the adults are not complete (Tables 3 and 4). Other factors which may affect adult survival before oviposition were not determined because of the mobility of this stage.

Table 3. Life table of one generation of *A. websteri* at Curlew Valley study site, 1971

x	l_x	d_xF	d_x	100 q_x
Age interval	No.* alive at beginning of x	Factor responsible for d_x	No.* dying during x	d_x as percentage of l_x
Larvae				
Period 1	37	Failure to establish and other **	7	18.92
Period 2	30	*Apanteles cacoeciae*	<1	
		Phyllobaenus sp.	<1	
		Temelucha sp.	1	
		Unknown	2	
		Total	4	13.33
Period 3	26	*Orgilus ferus*	10	
		Diadegma sp.	<1	
		Copidosoma bakeri	<1	
		Phyllobaenus sp.	1	
		Microsporidia	2	
		Unknown	3	
		Total	16	55.17
Pupae	10	*Phaeogenes* sp.	2	
		Spilochalcis leptis	1	
		Microdontomerus sp.	<1	
		Phyllobaenus sp.	1	
		Microsporidia	<1	
		Unknown	1	
		Total	5	50.00
Adults	5	Physiological causes	1	
		Microsporidia	<1	
		Sex Ratio ≈ 1:1		
		Total	1	20.00
Generation totals			33	89.19

Generation survival (S_G) = 0.11

* Number per kg fresh sagebrush
** Miscellaneous factors such as predation, misadventure and physiological causes

Explanation of symbols:

x - Age interval at which the sample was taken.
l_x - The number surviving at the beginning of the stage noted in the x column.
d_x - The number dying within the age interval stated in the x column.
d_xF - The mortality factor responsible for d_x.
$100q_x$ - Percentage mortality.

Table 4. Life table of one generation of *A. websteri* at Curlew Valley study site, 1972

x	l_x	d_xF	d_x	100 q_x
Age interval	No.* alive at beginning of x	Factor responsible for d_x	No. ** dying during x	d_x as percentages of l_x
Larvae				
Period 1	209	Failure to establish and other **	34	16.27
Period 2	175	*Apanteles cacoeciae*	18	
		Phyllobaenus sp.	2	
		Temelucha sp.	1	
		Competition and overpopulation factors	5	
		Total	26	14.86
Period 3	149	*Copidosoma bakeri*	4	
		Orgilus ferus	2	
		Diadegma sp.	<1	
		Phyllobaenus sp.	1	
		Microsporidia	8	
		Competition and overpopulation factors	21	
		Total	36	24.16
Pupae	113	*Spilochalcis leptis*	9	
		Phaeogenes sp.	6	
		Microdontomerus sp.	<1	
		Phyllobaenus sp.	1	
		Total	16	14.16
Adults	97	Physiological causes	7	
		Microsporidia	5	
		Sex Ratio ≃ 1:1		
		Total	12	12.37
Generation totals			33	59.33
Generation survival (S_G) = 0.41				

* Number per kg fresh sagebrush.
** Miscellaneous factors such as predation, misadventure and physiological causes.

See Table 3 for explanation of symbols.

Major mortality factors

Certain trends were apparent in the data compiled from 1971 to 1972. They show that moderate to heavy mortality occurred during the larval and pupal stages. Figure 6 compares the mortality of different age groups during the two field seasons. These data show that the fifth larval instar was the "crucial trial" period for the defoliator. High mortality during this period was brought about by the sequential action of parasites, disease and food shortage.

Parasites: Parasitism increased from 20 to 75% at the study site during 1971, but only from 12 to 24% in 1972 (Table 2). This reduction of parasitism resulted in a 500% increase in defoliator population. It would appear from these data that the parasite complex plays a major role in regulating defoliator density.

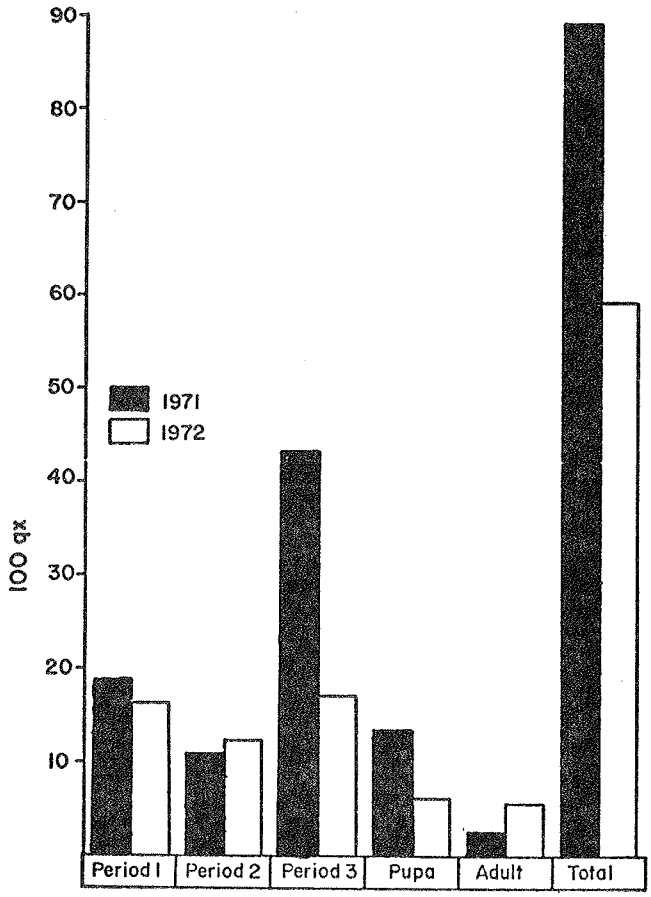

Figure 6. Mortality of *A. websteri* during five age intervals, Curlew Valley site, 1971 and 1972. For each year, 100 q_x values are based on the initial population.

Parasitism may also have caused indirect mortality by making the host more sensitive to catastrophic factors, thus increasing the host mortality prior to the emergence of the parasite.

Fillmore (1965) found some evidence that the ratio of hosts parasitized increased as the host density increased. This also appeared to be the case with the defoliator population at the study site, although the incidence of parasitism definitely lagged behind the host density in 1972. Functional responses of this type have also been observed for parasites of the spruce budworm (Miller, 1960) and the diamondback moth (Harcourt, 1969).

Disease: The microsporidian which infested the defoliator showed no indication of causing a significant population decline. The incidence of the protozoan was high enough in 1972, however, to cause 5% mortality of fifth instar larvae (Table 4). The occurrence of the protozoan was probably a result of defoliator overpopulation, although throughout the course of 1972 the disease remained at an enzootic level.

Competition and overpopulation factors: Several species of insects were found on sagebrush at the study site, such as: a lepidopteran leaf miner, *Bucculatrix tridenticola*; the garden case bearer, *Apterona crenulella*; the harvester ant, *Pogonomyrmex owyheei*; grasshoppers, and many unidentified moths. There is no evidence at present to suggest that these organisms compete directly with the defoliator for food.

Food shortage was evidently an important factor in the reduction of the defoliator population during the 1972 season. When sagebrush plants were completely stripped of foliage, larvae were frequently seen wandering about at the base of the plants. Defoliator mortality from the effects of food shortage was not directly determined, but represents the number missing which could not be accounted for by known mortality factors. Starvation was evidenced by the small size of many mature larvae and the frequent failure of larvae to pupate.

Food consumption and utilization

Figure 7 shows the mean food consumption and weight gain of 25 larvae during the 4th and 5th instars. These data indicate that the larvae ingested, on a dry weight basis, about 37 mg of sagebrush foliage. The mean fresh weight gain of larvae during the same period increased from 0.81 mg to 12.5 mg. The amount of food consumption was not determined for the first to third larval instars. However, an estimate from the body weight of newly-molted 4th instar larvae suggested that food consumption of these earlier instars would not exceed 3 mg. On this basis, the total food consumption for the entire duration of larval development would be about 40 mg of dry foliage or 80 mg of fresh foliage (based on a 50% dry weight).

The results of the utilization experiment involving fourth and fifth instar larvae are summarized in Table 5. The A.D., E.C.I. and E.C.D. indices indicate the insect's ability to gain weight with increased food consumption. These indices are relatively low when compared with other lepidopteran species (e.g., Waldbauer, 1968). Soo Hoo and Fraenkel (1966) suggested that plants with low water content tend to be inferior food and that this results in digestibility indices ranging between 25 and 35%. The high dry matter content of sagebrush leaves, ranging from 42 to 53%, and low digestibility indices of the defoliator, support this conclusion.

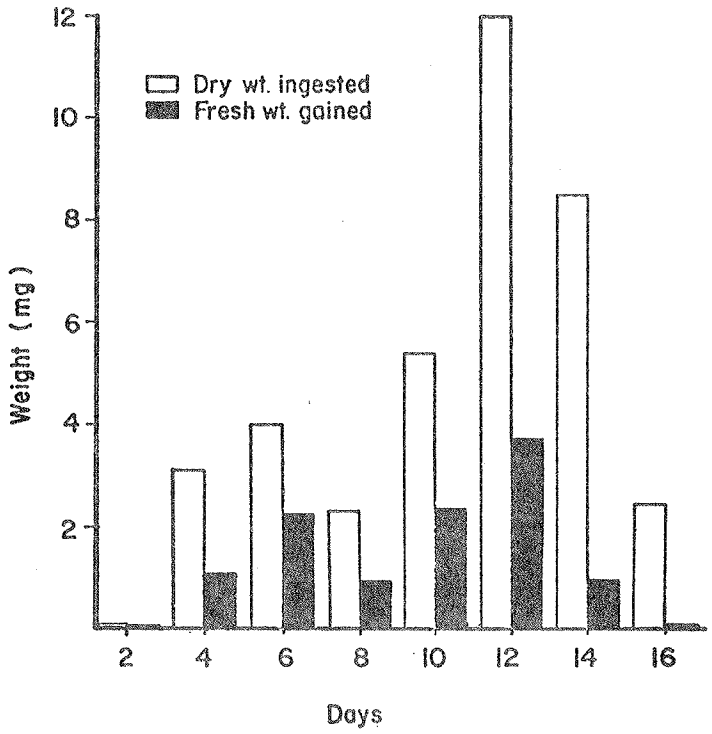

Figure 7. Mean food consumption and weight gain of *A. websteri* during the 4th and 5th larval instars. (DSCODE A3UHL04)

Table 5. Food utilization of 25 fourth and fifth instar larvae of *A. websteri* fed on sagebrush leaves (DSCODE A3UHL04)

	Duration of feeding period (days)	Dry weight consumed (mg)	Dry wt. gained (mg)	Fecal wt. (mg)	A.D. (%)	E.C.I. (%)	E.C.D. (%)	C.I.
Mean	16	37.0	3.1	24.1	34.9	8.4	24.0	0.4
Standard Error	1.1	3.3	0.8	1.2	1.8	0.8	1.6	0.1

A.D. = approximate digestibility.
E.C.I. = efficiency of conversion of ingested food.
E.C.D. = efficiency of conversion of digested food.
C.I. = consumption index.

Defoliation studies

In 1972 the defoliator population was more than five times larger than the previous year. As a result many plants were completely defoliated, and the overall damage was up to 80% in the study area. Most plants recovered from defoliation in the fall. Only 20 to 30% of the plants which were completely defoliated failed to produce new leaf buds.

Data obtained from sampling of defoliation of 26 randomly selected sagebrush plants are summarized in Table 6. Regression analysis of the relationship between percent defoliation and the sagebrush defoliator density revealed only a 5% correlation. It is likely that the lack of correlation was a result of sampling too late in the season for accurate estimation of the larval population which caused the damage. In the previous year the defoliator was rarely affected by factors such as food shortage and crowding, but in 1972 these factors caused high mortality. As a consequence, plants which were highly defoliated during June probably retained fewer larvae than plants that had sustained moderate to low defoliation. The presence of fewer larvae on the defoliated plants would have resulted in an underestimation of larval density.

Table 7 summarizes the findings on the effect of artificial introduction of defoliator larvae to caged plants. The results indicate that all caged plants suffered almost complete defoliation, regardless of the number of defoliators introduced. Introduction of 100 larvae to a caged plant resulted in a 91% recovery of defoliators. However, the addition of a higher number of defoliators to caged plants invariably reduced the defoliator recovery to a level between 28 and 39%. This fact emphasizes the importance of the role of food shortage in the defoliator ecology. On the basis of the results obtained from cage 1, it appears that each kg of sagebrush can support the development of not more than 240 defoliators.

Apterona crenulella

METHODS AND RESULTS

The number of degree-days required to initiate the spring emergence of overwintering first instar larvae of *A. crenulella* has been investigated in our laboratory. Overwintering old larval cases containing eggs were collected from the Green Canyon site near Logan on 29 January, 1972. Three constant temperature

incubators of 15.5, 21 and 26.5 C with a 16-hr photophase were used for this experiment. One hundred larval cases were placed in each incubator and the number of larvae that emerged each day was recorded. The temperature recorded for development was based on the time necessary to reach 50% larval emergence in the samples. Daily weather data were obtained from a weather station located near the study site. The results are graphically presented in Figure 8. The theoretical base temperature for larval emergence was calculated to be 10 C. The number of degree-days required for the larvae to emerge was calculated by subtracting the minimum development temperature from the incubation temperature, and multiplying this result by the number of days required for 50% larval emergence. The results indicate that 111 degree-days are required for initiation of larval emergence. A calculation of field temperature data showed that this degree-day was reached by late April. This is approximately the time when emergence of overwintering larvae was first observed in the field.

Table 6. Comparison of population density of *A. websteri* and percent defoliation of selected sagebrush plants at Curlew Valley site, July 1, 1972 (DSCODE A3UHL03).

Plant Number	Plant fresh wt. (kg)	No. of defoliators	Defoliators per kg sagebrush	Percent Defoliation
1	0.0845	59	70	71
2	0.1061	13	123	54
3	0.1760	42	239	47
4	0.1943	18	93	40
5	0.0455	28	615	96
6	0.0816	9	110	38
7	0.0726	34	468	93
8	0.1937	26	134	93
9	0.1002	16	159	80
10	0.1125	13	116	40
11	0.0895	9	101	98
12	0.1340	8	60	59
13	0.2246	17	76	78
14	0.1030	16	155	28
15	0.1287	32	249	91
16	0.1264	11	87	91
17	0.1626	22	135	23
18	0.0983	43	437	79
19	0.1138	11	97	73
20	0.0961	12	125	85
21	0.1007	14	139	82
22	0.0940	4	43	74
23	0.0990	10	101	21
24	0.1929	11	57	37
25	0.1158	41	354	98
26	0.1199	38	317	67

Table 7. Defoliation of caged sagebrush plants by four levels of introduced population of *A. websteri* larvae: Curlew Valley site, May 5 - July 1, 1972.

Cage No.	Plant fresh wt. (kg)	No. defoliators introduced	No. defoliators recovered	% defoliators recovered	% defoliation
1	0.4205	100	91	91	96.9
2	0.5025	200	56	28	98.5
3	0.4607	300	117	39	100.0
4	0.5260	400	118	30	100.0

Table 8. Effects of photoperiods on larval emergence of *Apterona crenulella*.

Photophase Duration (hr.)	Photophase		Scotophase		Total no. larvae emerged
	Mean no./hr photophase	%	Mean no./hr scotophase	%	
6	14.31	68.47	6.59	31.53	1227
8	8.14	72.74	3.05	27.26	1140
12	11.81	86.65	1.82	13.35	1307
14	12.82	86.98	1.92	13.03	1192

The effect of different day lengths on larval emergence was investigated by subjecting overwintering larval cases to photophases of 6, 8, 12 and 14 hr in incubators. The experiments were carried out at a temperature of 23.5 ± 1.5 C. Larval emergence was recorded at the beginning and the end of the photophases each day. The results are summarized in Table 8. The data show a direct correlation between the photophase duration and the mean number of larvae that emerged per hour of photophase. At a photophase of 14 hr, 87% of the larvae emerged during the day and 13% during the night. Even at a photophase of 6 hr, approximately 70% of the larvae emerged during the day. These data demonstrate that *A. crenulella* is a day-active species and that larval emergence occurs during the light period of the day. In order to determine the peak of larval emergence during a single day, larval cases were incubated at a 14 hr photophase and larval emergence was recorded at 2 hr intervals. Figure 9 summarizes the results of this experiment. The peak of larval emergence occurred within 2 hr after the initiation of the photophase. More than 90% of emergence was completed during the first 8-hr period. The remainder emerged before the end of the photophase.

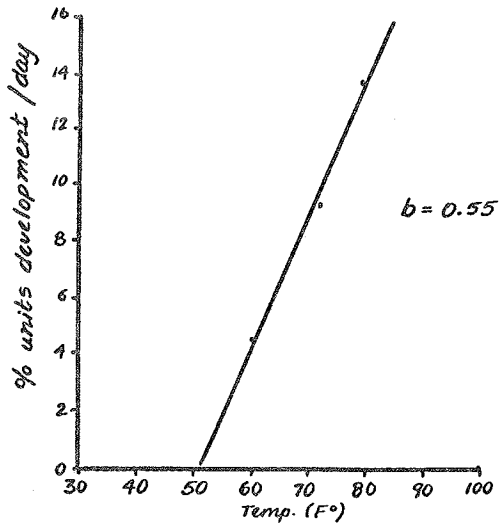

Figure 8. Percentage units of development/day of *A. crenulella* overwintering larvae.

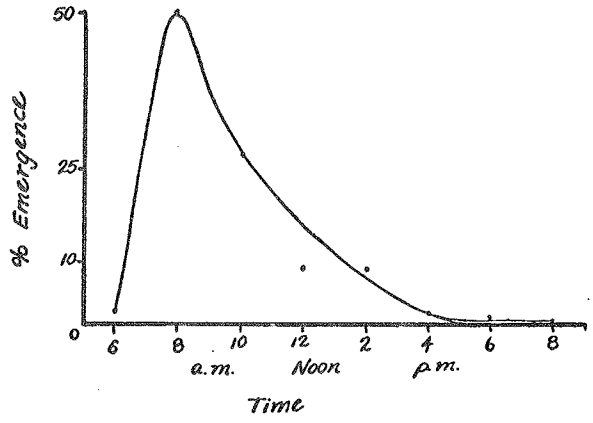

Figure 9. Time of larval emergence when kept in a 14 hr photoperiod.

Examination of a large number of larval cases collected in the field revealed an average of 16.3 eggs per case. An average of 15.3 larvae emerged from these cases, and infertility of 6.1% was indicated. Overwintering mortality was found to be very low in this species. Natural enemies include a clerid predator (*Phyllobaenus* sp.) and an unidentified hymenopterous parasite.

EXPECTATIONS

The population trend of the defoliator will be predictable when additional field data are compiled and analyzed. Two mortality factors, natural enemies and food shortage, exert major influences on the defoliator population. Detailed measurements of these mortality factors will provide accurate assessment of their relative importance in the regulation of population. Information on host range and degree of defoliation under field conditions will be available to assess the extent of sagebrush infestations. Laboratory studies will provide biological data that are essential inputs for the construction and improvement of life tables for this species.

Investigations on seasonal history and mortality factors of the garden casebearer will provide preliminary data on the ecology and population dynamics of this insect. Data on host range and feeding habits of the garden casebearer will be available to estimate the extent of defoliation of the big sagebrush as well as on other plants by this polyphagous insect. Biological data necessary for the construction of life tables will be supplied in the course of the study.

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